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Fecundity, Multiple Spawning, and Description of the Gonads in Sebastodes

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By

JOHN S. MacGREGOR

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By

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ABSTRACT

More than 50 species of Sebastodes, an ovoviviparous genus of scorpaenid fishes, occur off the California coast. In the ovaries of nine species examined, evidence of two spawnings per spawning season was found in three (S. ovalis, S. constellatus, S. paucispinis) but not in the other six (S. carnatus, S. rosaceus, S. serriceps, S. serranoides, S. atrovirens, S. ruberrimus). Two spawnings were indicated by either (1) small numbers of advanced larvae entrapped in the ovaries and associated with full complements of developing eggs or early embryos or (2) a secondary group of developing eggs along with about equal numbers of advanced embryos. The relative number of eggs or embryos was lower in the three species that gave evidence of two spawnings (162 eggs or embryos per gram of fish) than in the other six species (280 eggs or embryos per gram of fish).

INTRODUCTION

The rockfishes of the genus Sebastodes (family Scorpaenidae) support an important commercial and sport fishery along the coast of California, where more than 50 species occur (Phillips, 1964). These fishes are of special biological interest because they are ovoviviparous. Together with 18 species of viviparous Embiotocidae they contribute to a marine fauna that probably contains a higher proportion of species of live-bearing fishes than that in any other similar area in the world.

Estimating the seasonal fecundity of a fish species presents two primary problems. The first and easier problem is to determine the numbers and size distribution of yolked eggs in the ovary. The second and more difficult is to determine how many times the fish spawns during the spawning season.

Seasonal spawning in relation to the size distribution of yolked eggs within the ovaries may follow one of four patterns: (1) a bimodal (or multimodal) distribution of eggs in which spawning of the more advanced group is followed by development and spawning of one or more additional groups derived from the secondary group; (2) a bimodal distribution of eggs in which the most advanced group is spawned and resorption of the secondary group follows; (3) a unimodal distribution of eggs constituting the only spawning for that season; (4) a unimodal group of eggs which is spawned either shortly before or shortly after a secondary group is developed from the reserve of nonyolked egg cells. In this last situation, if a bimodal condition is present, it is present only when the advanced eggs are ripe or nearly ripe--unlike the more usual bimodal condition that is present from the earliest differentiation by size of the advanced group. In addition to the above four patterns, fish may develop eggs that are resorbed without spawning if the necessary environment or other spawning stimuli are absent.

Often where multiple spawning is suspected, evidence of previous spawning seems to disappear within a relatively short time. Fishes of the genus Sebastodes offer a unique opportunity to investigate some aspects of multiple spawning because they are live-bearers that have eggs of a type similar to the pelagic, nonadhesive eggs of many marine fishes.

MATERIALS AND METHODS

The rockfish examined for this paper were taken by the BCF (Bureau of Commercial Fisheries) research vessel, Black Douglas, on: January 20, 1961, at Forty-mile Bank, about 40 nautical miles west of San Diego, Calif.; March 3, 1961, at the Rockpile, about 20 nautical miles south of San Diego; and on April 11, 1961, at Tanner and Cortes

Banks about 100 nautical miles west of San Diego. R.H. Rosenblatt and C.C. Tuthill of Scripps Institution of Oceanography identified the rockfish taken January 20, and F.H. Berry of the then BCF California Current Resources Laboratory, La Jolla, Calif., identified those collected on March 3 and April 11.

The larger species of rockfish were measured and weighed fresh, and only the ovaries were preserved in formalin. The smaller species were preserved in formalin at capture. They were measured and weighed, and the gonads removed the following week at the laboratory.

After the ovaries were weighed and examined, the distributions of egg diameters were determined by the technique described by MacGregor (1957) for eggs of the Pacific sardine (Sardinops caerulea). Embryos were staged according to Ahlstrom's (1943) criteria for the Pacific sardine with the following exception: because rockfish embryos are more advanced than sardines at hatching, stage X was considered as extending from the end of Ahlstrom's stage IX to the beginning of eye-pigment formation, and stage XI from the beginning of eye-pigment formation to hatching. The numbers of eggs or embryos in each pair of ovaries were estimated by counting a weighed sample of the ovary under a binocular microscope and adjusting the count to the total ovary weight.

Tabular data on the female rockfish are presented as follows: Forty-mile Bank, table 1; Rockpile, table 2; Tanner and Cortes Banks, table 3. Additional data from the literature are compared to this study in table 4. Only the length and maturity data are available for some of the fish listed in table 2 that were used for physiological studies.

Table 1.--Data on eggs and embryos in the ovaries of female rockfish taken at Forty-mile Bank, January 20, 1961

Female rockfish			Ovaries		Eggs		Embryos		Embryos or eggs per gram of fish
Standard length	Total length	Weight	Weight	Percentage of fish weight	Number	Maximum diameter	Number	Stage	
Mm.	Mm.	Kg.	G.	Percent	Number	Mm.	Number	Number	Number
				Sebastodes pauciapinis					
590	695	3.5	148.0	4.2	731,811	0.72	--	--	209
495	590	2.15	246.0	11.4	--	--	388,399	XI	181
457	552	1.7	235.0	13.8	--	--	482,440	III-IV	284
455	545	1.7	189.5	11.1	--	--	361,062	IX	212
460	545	1.55	103.0	6.6	--	--	186,001	V	120
460	545	1.5	112.5	7.5	--	--	213,241	IV	142
455	540	1.5	47.84	3.2	205,130	0.66	--	--	137
435	520	1.45	222.0	15.3	--	--	512,497	II	353
450	540	1.4	29.22	2.1	335,765	0.54	--	--	240
440	530	1.4	41.90	3.0	250,866	0.62	--	--	179
435	520	1.4	200.0	14.3	--	--	425,038	VI	304
430	510	1.3	174.0	13.4	--	--	341,545	X	263
390	487	1.1	88.90	8.1	--	--	127,449	XI	116
				Sebastodes ruberrimus					
530	615	5.0	142.0	2.8	1,355,838	0.56	--	--	271
455	530	3.2	82.25	2.6	1,095,786	0.52	--	--	324
				Sebastodes serranoides					
372	450	1.35	256.0	19.0	--	--	445,623	X	330
				Sebastodes ovalis					
335	405	1.2	42.54	3.5	132,077	0.78	--	--	110
335	400	1.1	173.4	15.8	121,398	0.66	118,515	XI	110-108
320	384	0.9	40.79	4.5	115,458	0.86	--	--	128
305	365	0.8	47.89	6.0	--	--	70,614	X	88
292	345	0.75	42.01	5.6	114,151	0.96	--	--	152
				Sebastodes rosaceus					
196	235	0.240	6.99	2.9	66,761	0.62	--	--	278
191	229	0.198	6.94	3.5	62,992	0.70	--	--	318

Table 2.--Data on female rockfish taken at the Rockpile, March 3, 1961

Species of Sebastodes	Standard length	Total length	Weight	Gonad Weight	Egg		Embryo		Embryos or eggs per gram of fish	Gonad weight as a percentage of fish weight
					Number	Maximum diameter	Number	Stage		
	Mm.	Mm.	Kg.	G.	Number	Mm.	Number	Number	Number	Percent
S. carnatus	216	259	0.355	42.894	--	--	95,704	X	270	12.1
Do.	217	265	0.339	19,491	104,101	0.86	--	--	307	5.7
Do.	190	231	0.281	30,363	--	--	67,982	IV-V	242	10.8
Do.	185	226	0.251	6.386	44,118	0.86	--	--	176	2.5
Do.	217	262	--	--	--	0.86	--	--	--	--
Do.	215	259	--	--	--	--	--	XI	--	--
Do.	195	235	--	--	--	0.86	--	--	--	--
Do.	187	227	--	--	--	--	--	II	--	--
Do.	177	216	0.202	0.262	--	--	--	--	--	0.13
S. serriceps	237	285	0.362	21.452	69,599	1.00	--	--	192	5.9
Do.	225	268	--	--	--	0.52	--	--	--	--
Do.	214	262	--	--	--	0.48	--	--	--	--
Do.	196	238	0.250	--	--	0.70	--	--	--	--
S. atrovirens	263	318	0.416	10.888	143,156	0.62	--	--	344	2.6
Do.	251	311	0.454	20.251	182,890	0.76	--	--	403	4.5
Do.	227	277	0.299	2.010	--	0.42	--	--	--	0.67
Do.	215	267	0.299	3.117	--	0.50	--	--	--	1.04
Do.	242	296	--	--	--	0.54	--	--	--	--
Do.	246	300	--	--	--	0.58	--	--	--	--
S. constellatus	240	280	--	--	--	0.66	--	--	--	--
Do.	231	272	--	--	--	0.14	--	--	--	--
S. mystinus	258	302	--	--	--	0.16	--	--	--	--
Do.	195	203	--	--	--	0.12	--	--	--	--
S. vexillaris	258	311	--	--	--	0.62	--	--	--	--

Table 3.--Data on female rockfish taken at Tanner and Cortes Banks, April 11, 1961

Species of Sebastodes	Standard length	Total length	Weight	Gonad weight	Egg		Embryo		Embryos or eggs per gram of fish	Gonad weight as a percentage of fish weight
					Number	Maximum diameter	Number	Stage		
	Mm.	Mm.	Kg.	G.	Number	Mm.	Number	Number	Number	Percent
S. constellatus	295	353	0.800	46.37	--	--	120,824	II	151	5.8
Do	244	291	0.449	41.74	--	--	78,967	XI	176	9.3
Do.	257	305	0.554	62.88	--	--	105,510	X	190	11.3
Do.	244	290	0.370	42.92	--	--	71,928	XI	194	11.6
Do.	225	268	0.391	9.68	34,207	0.82	--	--	87	2.5
S. rosaceus	193	232	0.196	15.87	--	--	44,288	IX	226	8.1
Do.	189	224	0.163	2.76	37,044	0.56	--	--	227	1.7
Do.	181	220	0.184	7.26	--	--	26,344	III	143	3.9
Do.	169	203	0.142	9.77	--	--	33,371	X	235	6.9
Do.	150	184	0.119	7.87	--	--	24,822	X	209	6.6

Table 4.--Estimates of egg production of 20 species of Sebastodes

Species of Sebastodes	Fish	Weight range	Eggs per gram of fish		References
			Mean	Range	
	Number	Kg.	Number	Number	
S. ovalis	5	0.75-1.2	116	88-152	Present paper
S. jordani	10	0.046-0.275	131	83-182	Phillips, 1964
S. auriculatus	35	0.510-2.290	139	95-176	DeLacy, Hitz & Dryfoos, 1964
S. goodei	23	0.349-2.504	151	71-285	Phillips, 1964
S. constellatus	5	0.391-0.800	160	87-194	Present paper
S. crameri	12	0.617-3.062	165	51-237	Phillips, 1964
S. caurinus	33	0.283-2.608	183	38-301	Delacy et al., 1964
S. serriceps	1	0.362	192	--	Present paper
S. paucispinis	13	1.1 -3.5	211	116-353	Present paper
S. pinniger	1	2.722	220	--	Fraser, 1923
S. rosaceus	7	0.119-0.240	234	143-318	Present paper
S. carnatus	4	0.251-0.355	249	176-307	Present paper
S. entomelas	20	0.431-2.177	288	120-600	Phillips, 1964
S. flavidus	15	0.376-2.227	298	94-506	Phillips, 1964
S. ruberrimus	2	3.2 -5.0	300	271-324	Present paper
S. paucispinis	24	0.558-4.998	304	36-537	Phillips, 1964
S. ruberrimus	1	8.845	305	--	Clemens and Wilby, 1949
S. diploproa	15	0.118-0.776	312	112-502	Phillips, 1964
S. serranoides	1	1.35	330	--	Present paper
S. miniatus	12	0.517-2.631	347	122-618	Phillips, 1964
S. atrovirens	2	0.416-0.454	374	344-403	Present paper
S. saxicola	13	0.068-0.490	415	169-931	Phillips, 1964
S. pinniger	10	1.619-4.441	470	161-815	Phillips,1964

SPAWNING SEASON

Some information on the spawning season can be had from data on the collection of Sebastodes larvae in plankton net hauls (table 5) in the survey area of CalCOFI (California Cooperative Oceanic Fisheries Investigations)--Oregon to the southern tip of Baja California--for 1950-57 (Ahlstrom, 1952, 1953, 1954, 1958, 1959; Ahlstrom and Kramer, 1955, 1956, 1957). The species of larvae were not separated; as a group they constituted 7.6 percent of all larvae taken (average for 1955, 1956, and 1957). Their numbers were exceeded only by the larvae of northern anchovy (Engraulis mordax) and Pacific hake (Merluccius productus). In 1950-52, the number of Sebastodes larvae per haul averaged 13.9 and the peak of larval abundance was in April (2 years) and March (1 year). In the following 5 years Sebastodes larvae per haul averaged 25.1 and the peak of larval abundance came earlier, in February (4 years) and January (1 year). Rockfish clearly tend to spawn in winter; during the 8 years, the first 4 months of the year accounted for 68 percent of all Sebastodes larvae taken.

Other studies have also indicated that rockfish tend to spawn primarily in winter. Fitch (1958) recorded the hatching season of Sebastodes paucispinis as December through April and of S. miniatus and S. serrnoides as December through March. Wales (1952) gave the hatching season of S. mystinus as November through March. Clemens and Wilby (1949: 206), referring to young Sebastodes along the Canadian Pacific coast, stated, "These are less than 1/2 inch in length and are produced in large numbers during the summer months."

Table 5.--Rockfish spawning by months as indicated by Sebastodes larvae taken in plankton net tows at CalCOFI station off of the coast of California and Baja California, 1950-57

Month	1950-52				1953-57				1950-57			
	Stations	Larvae collected		Percentage[1] of total spawning	Stations	Larvae collected		Percentage[1] of total spawning	Stations	Larvae collected		Percentage[1] of total spawning
		Total	Per haul			Total	Per haul			Total	Per haul	
		Number	Number	Percent		Number	Number	Percent		Number	Number	Percent
January	218	4,161	19.1	12.6	511	22,305	43.6	15.2	729	26,466	36.3	15.1
February	321	6,196	19.3	12.8	600	50,539	84.2	29.3	921	56,735	61.6	25.7
March	402	8,437	21.0	13.9	729	32,436	44.5	15.5	1,131	40,873	36.1	15.1
April	421	12,627	30.0	19.9	923	26,721	29.0	10.1	1,344	39,348	29.3	12.2
May	443	5,822	13.1	8.7	1,054	15,494	14.7	5.1	1,497	21,316	14.2	5.9
June	483	5,840	12.1	8.0	1,063	10,521	9.9	3.4	1,546	16,361	10.6	4.4
July	423	3,931	9.3	6.2	854	8,526	10.0	3.5	1,277	12,457	9.8	4.1
August	322	2,171	6.7	4.4	313	2,242	7.2	2.5	635	4,413	6.9	2.9
September	309	646	2.1	1.4	158	659	4.2	1.5	467	1,305	2.8	1.2
October	175	734	4.2	2.8	470	2,827	6.0	2.1	645	3,561	5.5	2.3
November	180	1,120	6.2	4.1	147	2,595	17.7	6.2	327	3,715	11.4	4.8
December	64	510	8.0	5.3	368	5,914	16.1	5.6	432	6,424	15.2	6.3
Total or average	3,761	52,199	13.9	--	7,190	180,770	25.1	--	10,951	232,974	21.3	--

[1]Percent spawning is weighted to the number of stations in that month.

DESCRIPTION OF THE OVARIES AND EGGS

The ovaries are sac-shaped, of about equal size, and slightly joined posteriorly. Those containing yolked eggs or early embryos are yellow, except that some ovaries of Sebastodes paucispinis tend to be cream-colored. Ovaries that contain late embryos (stage XI) become dark gray owing to the formation of larval pigment, especially in the eyes.

Variations Among Ovaries of Different Species of Sebastodes

The ovaries of three species--S. paucispinis, S. ovalis, and S. constellatus--contained remains of larvae from the previous spawning. Most ovaries of S. paucispinis and S. ovalis that contained embryos or unfertilized eggs also had dark blotches or spots just under the tissue of the ovarian envelope. In at least some specimens this dark material was composed of pigment spots of advanced larvae from a previous spawning that had failed to escape from the ovary upon hatching. The yolk sacs of all these larvae were almost completely absorbed, and the larvae were developed beyond the stage at which they are normally released. In some ovaries the larvae were intact and in good condition (fig. 1); in others they were disintegrating; and in still others only the pigmented lenses of the eyes remained (fig. 2).

Advanced larvae, more or less intact, from the previous spawning were found in 6 of the 13 S. paucispinis studies and were associated with early embryos and unfertilized eggs. Four contained questionable larval remnants, and no traces of larvae were found in the remaining three; embryos were more advanced in these seven ovaries than in the other six.

Four of five S. ovalis contained larvae from the previous spawning with the developing eggs or embryos. The ovaries of the fifth contained a full complement of embryos on the verge of hatching and a group of unfertilized eggs near maturity. The estimated number of embryos was 118,000, and the number of eggs 121,000. Figure 3 shows stage XI embryos and unfertilized eggs from this fish.

Of five S. constellatus taken on April 11, three contained stage X and XI embryos and a secondary group of unfertilized yolked eggs about equal in numbers to the primary groups of eggs containing embryos. Diameters of these smaller eggs were 0.20 to 0.46 mm. Neither of the remaining two specimens had secondary groups of yolked eggs, but one that contained stage II embryos also had black pigment spots that may have been larval remnants within the ovary, and one containing advanced unfertilized eggs also contained one advanced larva, in good condition, from a former spawning. No evidence of previous spawning appeared in the ovaries of the three specimens that contained the secondary modes of eggs.

None of the other species of Sebastodes examined contained larvae such as those found in the above three species. The ovaries of all species had small eggs less than 0.20 mm. in diameter, without yolks. The ovaries of two S. mystinis, one 272-mm. S. constellatus taken March 3, and one--the smallest--S. carnatus contained only this type of egg.

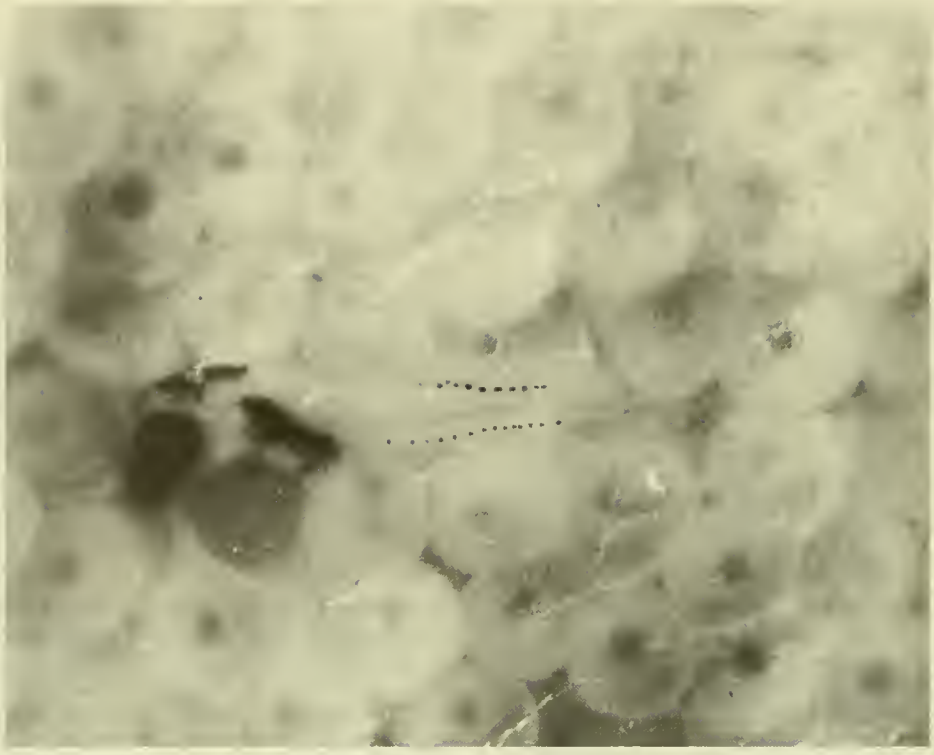

Figure 1.--Sebastodes ovalis--nearly ripe eggs and entrapped larva from the previous spawning as seen through the tissue enveloping the ovary.

Figure 2.--Sebastodes ovalis--stage X embryos and pigmented lenses of the eyes of entrapped larvae from the previous spawning.

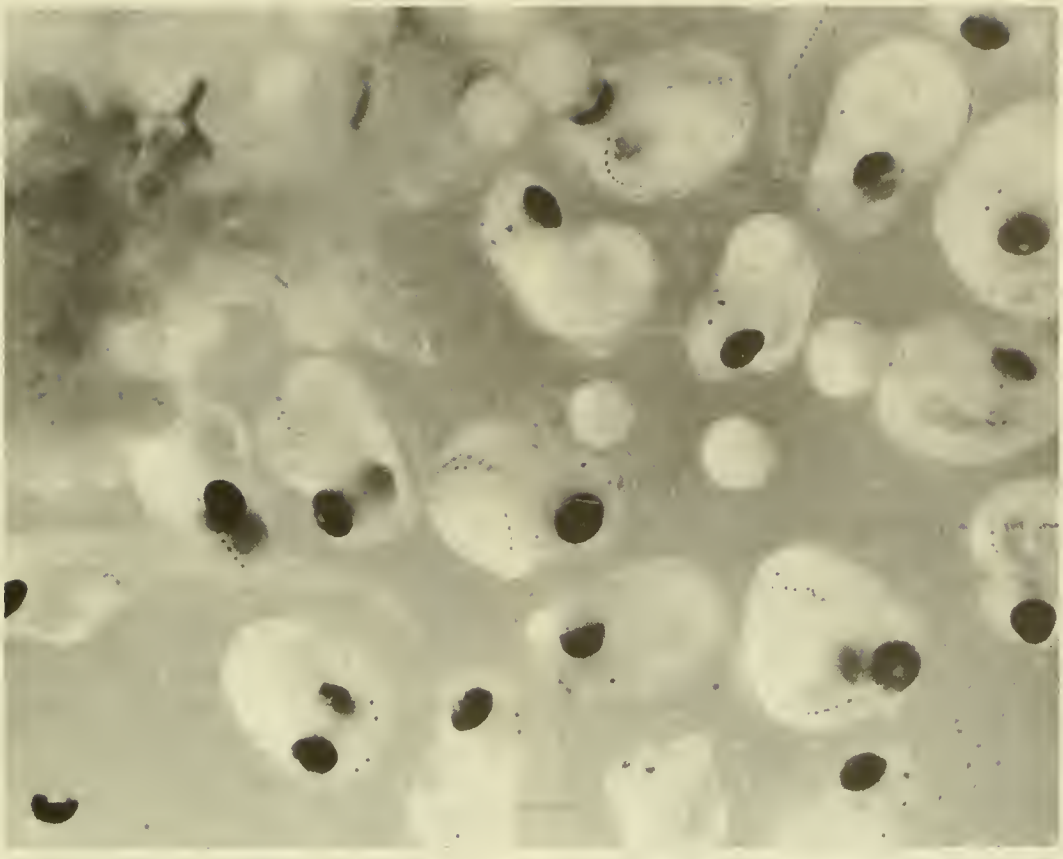

Figure 3.--Sebastodes ovalis--stage XI embryos and unfertilized eggs of the subsequent spawning batch.

These fish were probably immature, although it is possible that the ovaries were in a resting condition rather than immature. The other fish contained a single group of either yolked eggs or embryos (except for the one S. ovalis and three S. constellatus mentioned above, which contained both).

A few fish that had yolked eggs also contained a secondary group of yolked eggs smaller than the main group of developing eggs. (An example of this size distribution of a group of such eggs--0.20 to 0.44 mm. diameter--is shown in the frequency distribution plotted in figure 5A.) These eggs, however, were not considered as part of a batch to be spawned. Howard and Landa (1958), who found similar distributions of eggs in the anchoveta (Cetengraulis mysticetus), concluded that these smaller eggs were not spawned. To be considered as a possible subsequent spawning group, the number of these smaller eggs should about equal or exceed that of the more advanced group. This condition is frequently found in other species of fish. The number of these secondary eggs did not exceed that of the primary group in any of the Sebastodes specimens examined (except for the S. ovalis and S. constellatus specimens containing about equal numbers of stage X or XI embryos and rather well-developed eggs); and in practically all fish the small eggs equalled only a small fraction of the primary group or were absent from the sample examined.

The above findings indicate that at least some individuals of S. paucispinis, S. ovalis, and S. contellatus spawn two batches of larvae a season; these three species generally produced distinctly smaller numbers of eggs per batch than the species that appear to spawn only once per season. The average relative fecundities (eggs or embryos per gram of fish) of the three species were as follows: S. ovalis, 116; S constellatus, 160; and S. paucispinis, 211 (mean, 162). For six species that showed no evidence of more than one spawning the averages were as follows: S. serriceps (only one specimen available), 192; S. rosaceus, 234; S. carnatus, 249; S. ruberrimus, 300; S. serranoides, 330; and S. atrovirens, 374 (mean, 280).

The mean relative fecundity of S. ovalis and of the five S. constellatus collected on April 11, all of which showed evidence of

two spawnings, was 138 or about half of the mean of the other six species. In S. paucispinis, in which some specimens gave evidence of two spawnings and some did not, the relative fecundity was about midway between the two groups. No relation was detected within the species S. paucispinis, between evidence of two spawnings and relative fecundity. The group of six specimens that showed evidence of two spawnings and the group of three that did not each had average relative fecundities of 219; the four questionable speimens had an average relative fecundity of 192.

The association of secondary groups of unfertilized yolked eggs with only stage X and XI embryos indicates that the secondary group does not begin to develop until the primary group is much advanced. I have also found this condition in the oviparous species, Vinciguerria lucetia, in the developing ovaries of which only one group of yolked developing ova is present unless this group is almost ripe; then, a secondary group of smaller yolked ova, in numbers about equal to the primary group, may often be found. In many species of fish the secondary group of yolked ova is present throughout most of the development of the primary group but shows little growth, especially when measured by volume rather than diameter, until the primary group is almost ripe or has been spawned. In the oviparous species, Cololabis saira, the secondary group of yolked ova may out-number the primary group 10 or 20 times. From this numerous secondary group a second spawning batch about equal in number to the primary group will develop, but only when the primary group is ripe or nearly ripe.

In some species of fishes a secondary group of yolked eggs may be resorbed after the spawning of the primary group; in others the secondary group may furnish one or more subsequent spawning batches; and in still others either condition may prevail depending on age, size, or condition of the fish or the environment.

The evidence of entrapped larvae in association with fertilized eggs in the ovaries of the three species of Sebastodes is almost conclusive proof of at least two spawnings per season in these species. The absence of entrapped larvae does not necessarily prove that the other species do not spawn more than once, although it offers a strong indication. A greater time interval between spawnings in some species would allow more time for the disintegration of larvae, and the absence of a developing group of secondary eggs at hatching time might allow all larvae to escape from the less crowded ovary.

None of the authors listed in table 4 mentioned evidence of multiple spawning in the species they examined, although a few of the species seem to have rather low relative fecundities. In the present study, with the exception of S. ovalis, S. constellatus, and some S. paucispinis (table 1, 2, and 3), the relative fecundity approximates the range of 200 to 400 eggs per gram of fish typical of many marine fishes of similar size that spawn nonadhesive, pelagic eggs. The fertilized Sebastodes egg more closely resembles such eggs than do those of any other live-bearing species.

The Live-Bearing Trait in Fishes

A number of families of fishes other than the Scorpaenidae include species that bear living young. Eigenmann (1894: 404) stated:

> At least two types of viviparity may be distinguished in fishes: first, those in which the yolk furnishes all the intraovarian food (Poecilia, Gambusia, Scorpaenidae); and second, those in which the greater part of the food is furnished by the ovary (Blennis, Anableps, and Embiotocidae).
>
> In the first type the number of young is usually not less than in related oviparous forms, while the number of young in the second is always greatly reduced.

In addition to the Poecilidae, Scorpaenidae, Blennidae, and Embiotocidae mentioned by Eigemann, the live-bearing trait is found in the Hemiramphidae and Zoarcidae. In the Hemiramphidae, generally saltwater forms such as Hemiramphus and Hyporhamphus are oviparous but generally fresh-water forms such as Zenarchopterus and Dermogenys are live-bearing (Smith, 1945). In the Zoracidae, Zorces viviparus of the eastern North Atlantic is viviparous, whereas Zoarces anguillaris of the western North Atlantic spawns large demersal adhesive eggs (Bigelow and Schroeder, 1953).

Eggs of Oviparous Scorpaenids

The available data indicate that the oviparous scorpaenids are pelagic spawners. Okada (1955) reported that the scorpaenid, Hydrodytes rubripinnis, spawns pelagic eggs 0.8 to 0.9 mm. in diameter in July and August. Fitch (1958), who reported that Scorpaena guttata spawns from April through August, described a modification unique to this genus. "The eggs are imbedded in the gelatinous walls of hallow, pear-shaped, egg-balloons. The paired egg-balloons, each 5 to 10 inches long are joined at their small ends. The walls of these 'balloons' are about one-tenth inch thick, transparent or greenish in color and contain a single layer of eggs. The eggs are about one-twentieth inch each in diameter. The 'balloons' are spawned at the bottom of the sea and rise rapidly to the surface. The eggs hatch at the surface within 5 days."

Artifactual and Natural Aberrations Among Eggs in Sebastodes

Certain embryonic stages were considerably distorted by the formalin used in preservation. Many eggs containing embryonic stages II through V were larger than others from the same ovary, although the embryos in the size groups of eggs appeared identical (table 6, fig. 4). This condition appeared to be caused by the rupturing of the yolk membrane, owing to the osmotic effects of the preservative, whereas the egg membrane remained intact. From 25 to 39 percent of the stage II to V eggs were affected in fish containing these stages. None of the eggs of stages VI to XI were affected. It may be relevant that blastopore closure takes place at stage V. The greater fragility of early-stage eggs has been observed in other fish species (Ahlstrom and Ball, 1954).

Table 6.--Sebastodes paucispinis--embryonic stage, egg diameter, and embryos per gram of ovary

Embryonic stage	Median egg diameter		Embryos per gram of ovary
	Intact yolks	Ruptured yolks	
Number	Mm.	Mm.	Number
II	0.78	0.90	2,309
III-IV	.80	.98	2,053
IV	.78	.96	1,880
V	.78	1.04	1,806
VI	.78	--	2,125
IX	.78	--	1,905
X	.82	--	1,963
XI	--	--	1,579
XI	--	--	1,434

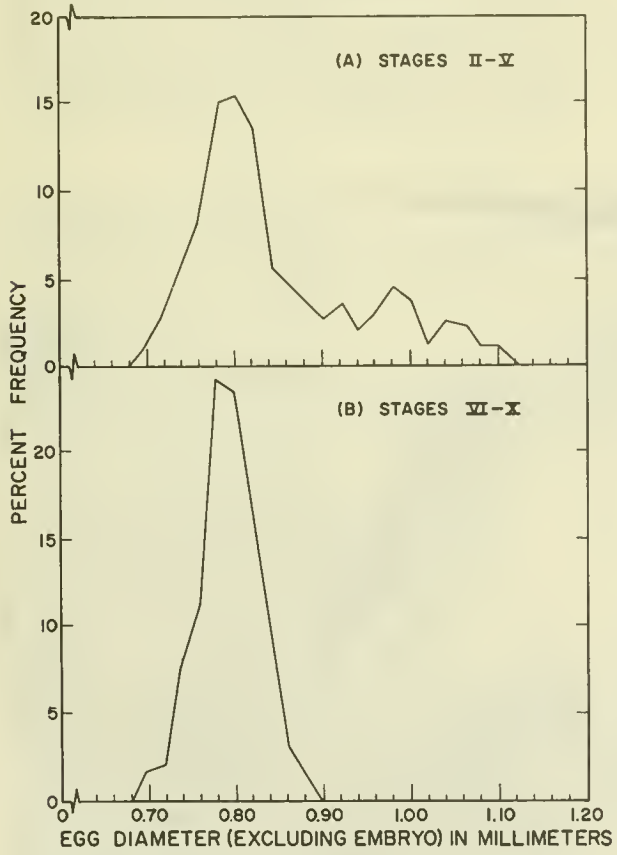

Figure 4.--Diameter frequencies of fertilized eggs from the ovaries of Sebastodes paucispinis showing the effect of formalin preservation before (A) and after (B) blastopore closure.

Another type of aberrant Sebastodes egg in ovaries containing embryos consisted of unfertilized or undeveloped eggs of the same original batch as the developing embryos. These eggs contained a ruptured yolk membrane, had yolk material of uniform texture distributed within the egg membrane, had a normal oil globule, and were 1.20 to 1.84 mm. in diameter. A pooled sample of embryos from several specimens of S. paucispinis contained 23,146 embryos and 14 (0.06 percent) unfertilized or undeveloped eggs. These eggs were found in all species that contained embryos.

Formalin may also cause swelling in ripe, unfertilized eggs. The diameters of intact, ripe, unfertilized eggs of most of the species, of Sebastodes averaged about 0.80 mm. Those of S. rosaceus were smaller--average about 0.65 mm. The female S. serriceps contained a group of eggs that averaged 0.94 mm. and were 0.86 to 1.00 mm. in diameter--the largest unfertilized eggs found in any of the specimens. Because no other comparable material for this species appeared in the collections, the amount of possible swelling caused by preservation is not known.

The diameters of the yolks of newly fertilized eggs and stage X embryos are closely similar (except as affected by preservation artifacts). One specimen of S. ovalis contained unfertilized eggs that averaged 0.91 mm. and were 0.80 to 0.96 mm. in diameter (fig. 5C). Most of these, except for a few 0.80 to 0.84 mm. in diameter, seemed to have ruptured yolk membranes, although this condition is difficult to detect because of the darkness of the yolk material in unfertilized eggs preserved in formalin. In another specimen of S. ovalis containing stage X embryos the diameter of the area enclosed by the yolk membrane averaged 0.80 mm. and ranged from 0.72 to 0.88 mm. (fig. 5A-D).

To study the relation between yolk size of embryos, I determined the number of embryos per gram of ovary and measured the diameters of eggs for the various embryonic stages in the ovaries of the nine specimens of S. paucispinis. The thickness of the embryo was not included in the egg diameter, and as the perivitelline space is not developed, the "intact yolk" egg diameters are, for practical purposes, also yolk diameters. (Stage XI embryos, which have oval yolks, are difficult to measure accurately.) The volume enclosed by the yolk membrane did not decrease as the embryos increased in size (table 6). This fact is also shown by the decrease in embryos per gram of ovary as the embryos

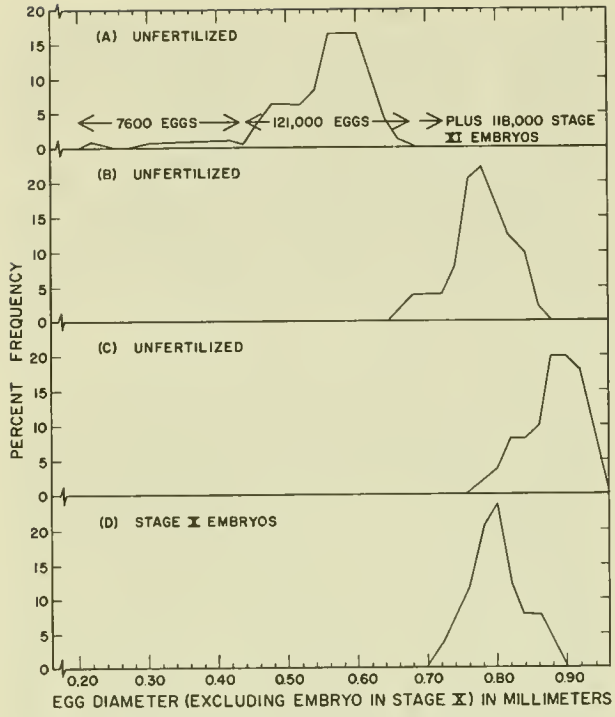

Figure 5.--Diameter frequencies of eggs from the ovaries of Sebastodes ovalis--(A) unfertilized developing eggs before release of advanced embryos, (B) nearly ripe eggs with intact yolks, (C) ripe unfertilized eggs with ruptured yolks, (D) stage X embryos.

develop. The increased size of eggs with ruptured yolk is reflected in the relatively low number of embryos per gram for stages II through V. Embryos per gram for these stages should probably be about 20 to 30 percent higher.

Because fertilized rockfish eggs lack follicles, the yolk cannot be replenished. Water or other fluid probably replaces the yolk used by the developing embryo. Consequently the apparent volume of the unsegmented yolk remains the same while the weights of embryo and egg increase. The same condition appears to prevail in fish eggs that develop pelagically. The size of the yolk of the fertilized egg, therefore, indicates the size of the unfertilized ripe egg which has no perivitelline space.

DESCRIPTION OF THE TESTES

The testes of male rockfish captured on January 20, 1961, were relatively much smaller than those of breeding males of most other species of fish. Although the testes are surrounded by the urinary bladder where they join the genital papilla (fig. 6), they apparently do not enter the bladder. In most specimens the bladder was filled with a clear fluid, but in one freshly caught specimen of S. paucispinis the fluid was milky. Slight pressure on the bladder caused the

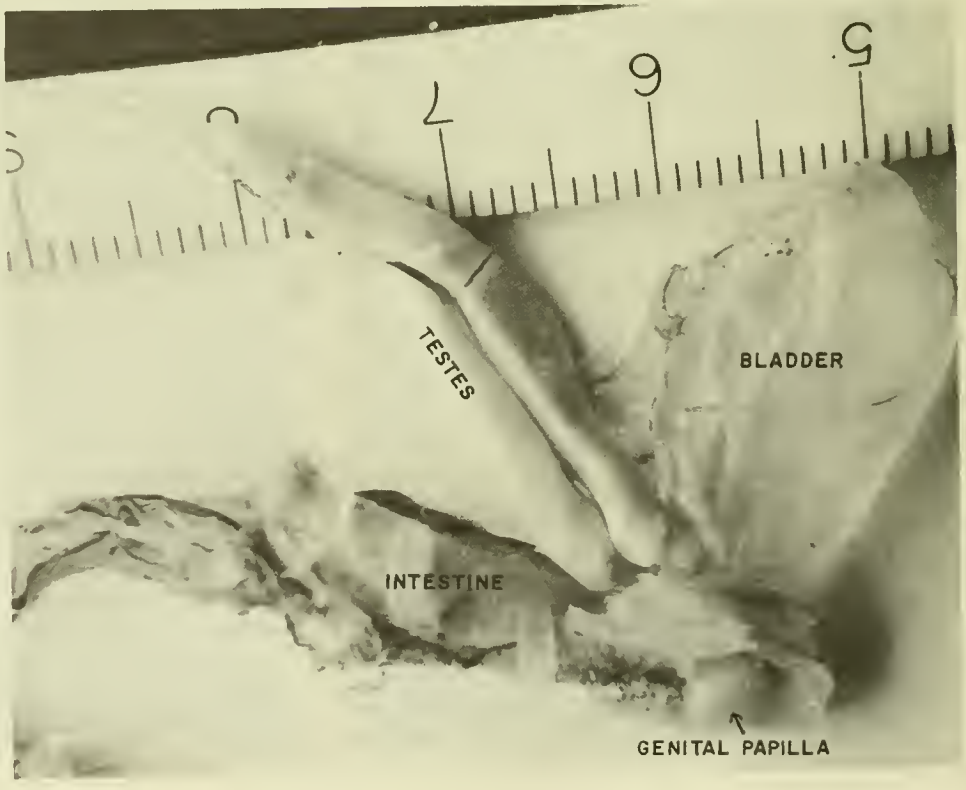

Figure 6.--Testes, bladder, genital papilla, and part of the intestine of Sebastodes serriceps (scale in millimeters).

fluid to be ejected through the genital papilla with considerable force. Eight specimens representing five species of Sebastodes, preserved in formalin and examined in the laboratory, all appeared to have ripe testes; except for the one specimen of S. vexillaris; however, the bladders contained only clear fluid. In the S. vexillaris it appeared that some testicular material having the consistency of putty had moved into the base of the bladder, and the bladder itself contained some whitish fluid. Although it is possible that the bladder functions to store, dilute, or ejaculate the sperm, it is probable that the conditions noted in the single specimens of S. paucispinis and S. vexillaris were artifacts caused by the pressure changes undergone by the fish in being hauled to the surface.

The relative gonad weight (weight of gonads as a percentage of weight of fish) for eight males was very low (table 7). The relative gonad weights of the females (tables 1, 2, and 3) were much higher and similar to other marine fishes in this size range. Among other species of fish the relative gonad weights of males and females are more closely similar during the spawning season.

The small size of the testes may be the result of partial spawning, as the spawning season was well advanced at the time of capture. Most of the females of the five species represented by the male contained unfertilized ova, however, as did most females of the other species. Also, none of the many males examined at sea had noticeably enlarged gonads. The reduced size of the testes may be related to the presumed greater efficiency of internal fertilization.

CONCLUSIONS

Of nine species of Sebastodes examined three--S. ovalis, S. constellatus and S. paucispinis--showed evidence of two spawnings per year. Two lines of evidence were found: (1) small numbers of advanced larvae entrapped in the ovaries along with full complements of developing eggs or early embryos; (2) a secondary group of developing eggs in the ovaries with about equal numbers of advanced embryos. No evidence of two spawnings was found in the ovaries of the other six species.

The relative fecundity (number of eggs or embryos of a single spawning batch per gram of fish) averaged 162 for the three species that gave evidence of two spawnings and 280 for the six species that gave no evidence of two spawnings. In the species that spawn twice the development of the second spawning batch appears to be inhibited until the first batch is fertilized.

Table 7.--Data on length, weight, and weight of testes of rockfish

Species of Sebastodes	Standard length	Total length	Weight	Weight of testes	Weight of testes as percentage of fish weight
	Mm.	Mm.	G.	G.	Percent
S. serriceps	215	251	311	0.456	0.15
S. atrovirens	250	306	426	1.099	.26
S. atrovirens	227	277	306	1.058	.35
S. vexillaris	285	345	612	1.521	.26
S. rosaceus	177	214	166	.178	.11
S. rosaceus	172	210	191	.170	.09
S. rosaceus	184	224	208	.198	.10
S. constellatus	240	429	285	.906	.32

Eigenmann (1894) in his study of the viviparous embiotocid, Cymatogaster aggregatus, found that the two sexes were completely out of phase in the ripening of gonads. The males ripen in the spring, and copulation takes place at that time, following parturition. The sperm is stored by the females until they ripen the following fall. This situation probably does not exist among the ovoviviparous species of Sebastodes. The eggs are fertilized when ripe and are merely retained in the ovaries until they hatch.

The weight of the eggs containing embryos increases as the embryos develop, even though the eggs are no longer connected to the ovarian tissue. The volume enclosed by the yolk membrane does not decrease as the embryo develops, apparently because the yolk used by the developing embryo is replaced by outside fluids.

Preservation in formalin caused some swelling of ripe, unfertilized eggs and fertilized eggs in the stages of development preceding that of blastopore closure. Developing eggs that were not ripe and fertilized eggs after blastopore closure did not seem to be adversely affected. Swelling of eggs was accompanied by rupturing of the yolk membranes, although the egg membrane remained intact.

The size of the ripe testes of male rockfish, which are closely associated with the urinary bladder, are greatly reduced compared to those of most other species of fish.

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